Using Flow Gauges to Determine Leaf Specific Conductance in Hybrid Poplars Under Mesic and Xeric Conditions.

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Abstract

A study was conducted using sap flow gauges to determine leaf specific conductance (LSC) in hybrid poplars in an environmentally-controlled greenhouse at Swift Current, Saskatchewan. Sap flow rates were compared between CanAm and Walker poplar clones using stem flow gauges. The primary objectives were to verify differences in LSC observed between the clones under moist field conditions in a previous study and to compare the responses in sap flow and LSC within these trees as imposed soil conditions changed from moist to dry. Walker poplars appear to be well-suited to mesic sites, and, under ample soil moisture, perform better than CanAms. However, they are susceptible to mid-season terminal shoot dieback, while CanAm poplars do not seem to be as susceptible. We suspect that this is primarily attributable to a greater LSC of CanAm poplars and possibly achieving better stomatal responses during periods of extended vapor pressure deficits. The gauges were mounted near the base of each tree. Following gauge installation, the trees were watered to field capacity. No additional water was added during the course of the test. Sap flow, leaf water potentials and tree conditions were monitored for 17 days as the soil conditions evolved from moist to dry. Results indicate that the CanAms displayed a greater LSC under moist as well as dry conditions compared to the Walkers. Throughout the testing period, CanAm mid-day leaf water potentials were slightly more negative than for the Walker poplars. Although CanAm poplars appear to be less water efficient than Walkers, they are better able to function and survive during periods of extended vapour pressure deficits.

Introduction

Recently, advancement in technologies have allowed researchers to investigate plant transpiration by measuring sap flow. This is done using flow gauges that are attached to the plant stems. The advantages of these gauges are that they do not disturb the plant root medium as many lysimeters do, are non-destructive, require no calibration, and have little affect on the transpiration behavior of the plant during measurement. Other advantages include: (1) that the proper installation and functioning of gauges can be ascertained, and the reliability of the measurements can be assessed by studying the raw data, (2) the potential accuracy resulting from a properly installed sap flow system under moderate sap flow conditions can be excellent, and (3) long-term observations are possible (Angadi et al. 2003). Several sap flow gauges employ the heat balance concept. The most popular has been a gauge based on initial designs by Sakuratani (1981); Sakuratani (1984), further refined by Baker and van Bavel (1987), and Steinberg et al. (1989), are currently available commercially under the label (Dynamax Corp., Texas).

Walker poplars favour mesic sites and, under good moisture conditions, perform better than CanAm poplars. However, the Walker trees are more susceptible than CanAm poplars to mid-season die-back of terminal shoots. This could be attributable to a greater leaf-specific conductance (LSC) (transpiration losses through the leaves) of CanAm poplars and/or better stomatal response of CanAms to high vapor pressure deficits. In a previous study conducted in a poplar plantation established in a mesic site near Swift Current, Saskatchewan, results showed that CanAm poplars had a significantly higher LSC than Walkers (Wall et. al. 2005). The data suggested that CanAms would be better able to meet the transpiration demands during warm summer days than Walkers, as CanAm flowrates increased at a significantly higher rate than Walkers with increasing temperatures (Wall et. al. 2005). Even under the generally mesic conditions characteristic of this site, Walkers displayed a higher rate of terminal shoot die-back (9.2 %) than CanAms (4.5 %) (unpublished data). Because conditions remained relatively cool and moist throughout the experiment, we could not demonstrate that CanAm poplars achieve better stomatal responses to high vapor pressure deficits and thus are less susceptible to mid-season dieback of terminal shoots. Therefore, a second study was initiated in an environmentally controlled greenhouse to verify field differences observed in LSC between the two poplar (Populus *deltoides* Bartr. X. P. *xpetrowskyana* Scneid.) clones, (Walker and CanAm), using the same heat-balance sap flow gauges used in the field experiment, and to compare the response in sap flow and LSC for these trees as soil moisture conditions evolve from mesic to xeric.

Materials and Methods

Theory and Operation of Sap Flow system

The gauges used in this experiment were Dynamax (Model SGA-10) stem flow gauges, (Dynamax Inc, Houston, TX, USA) and have been described in detail by Baker and van Bavel (1987), Steinberg et al. (1989), and Ham and Heilman (1990). A small flexible foil heater of fixed width completely encircles the stem or root and constantly emits heat energy, measured as a flux, to a small portion of the conductive tissue. Each heat balance gauge is fitted with foam covers, weather shields, and multiple layers of aluminum foil to reduce unwanted heat and radiative exchanges and ensure steady-state energy transfer. Assuming no energy storage within the gauge installation, the input of heat flux to the system (Q), electrically powered in joules per second, equals the sum of the outward or radial heat loss through the insulation shielding surrounding the gauge (Qr), the axial heat conducted in both directions (Qv), and the convective heat carried by the sap flow (Qf):

$$Q = Qr + Qv + Qf \qquad \text{[in joules per second]}$$

The fluxes Qr and Qv are calculated electronically in this gauge using measured temperature gradients, fixed coefficients, and the conductive cross-sectional area of the stem or root (Ac) in cm^2. With the assumption that the specific heat capacity (Cp) of the sap equals that of water at 25 ºC (4.18 joules per gram per ºC), and a measure of the temperature difference in the sap caused by Q moving into and out of the measurement reach (T_{out} - T_{in}), the Qf-flux can be converted to sap flow (F) in grams per second (or hour):

$$F = \frac{Qf}{Cp\,(T_{out} - T_{in})} \qquad \text{[in grams per second]}$$

Methods

Sap flow gauges were installed near the base of the main stem (below all leaves) of four Walker and four CanAm trees growing in 30 litre pots, measuring 380 mm top diameter with a depth of 300 mm. They were housed in Agriculture and Agri-Food Canada's Salt Tolerance Testing Laboratory (Steppuhn and Wall 1999), located at the Semiarid Prairie Agricultural Research Centre, in Swift Current, Saskatchewan. The trees were started from cuttings measuring about 250 mm in length in small containers containing peat moss only. Following the initiation of growth they were transferred to 30 litre pots containing a 1:1 packed mix of peat moss and Swinton silty loam top soil. The pots were watered manually with a 3 percent 20-20-20 water soluble fertilizer with chelated trace elements (Professional Gardener Co. L.T.D., Calgary Alberta, Canada) to maintain optimum growing conditions. A growth period of 95 days was required for the stems to reach the desired thickness to facilitate a good fit for the sap flow gauges (the Dynamax Model SGA-10 flow gauges used in this study required a nominal stem diameter of about 9 to 13 mm). At this time the respective plant heights averaged 1668 mm for the CanAms and 1725 mm for the Walkers (Table 5). The stem diameters (measured 200 mm above the base of the tree) were 9.0, 9.2, 8.5, and 9.3 mm for the CanAms and 10.1, 10.6, 10.4, and 10.0 mm for the Walker clones. The branches were fairly smooth and required minimum preparation for gauge attachment. Prior to installing the gauges, a thin layer of electrical insulating compound (G4, Dow Corning Corp., Midland MI) was applied to improve thermal contact and to protect the heater from water vapour condensation (Dynamax 2000). White foam insulation, foam 'O' rings above and below the gauges, and reflective-painted PVC weather shields were used to minimize temperature fluctuations around the gauges (Dynamax 2000). In addition, at least three layers of aluminum foil were wrapped around the installation to seal it from direct radiation (Angadi et al. 2003). Connecting wires were covered with aluminum foil near the gauges to avoid temperature fluctuations. Following installation, the portion of the branch above and below the gauge was sealed with electrical insulating compound to prevent moisture penetration. A constant 4.7 volts (which was gradually reduced to 4.0 volts as flow rates decreased) from a 12 V deep-cycle marine battery passed through a data logger transformer to each gauge. The effective branch thermal conductivity was assumed to be 0.42 W^{-1} $^{o}C^{-1}$, as suggested by Sakuratani (1981). The effective thermal conductivity of each gauge installation (Ksh) was estimated during low sap flow periods, from early morning observations (Dynamax 2000). When convective heat loss was less than 5% of the total heat supplied, flow rates were electronically set to zero. Gauge signals were scanned every 30 seconds using a data logger (Model 10X, Campbell Scientific, Logan Utah), and mean values were calculated every 30 minutes and stored. Following gauge installation, tree sap flow was monitored for several days under field capacity conditions to ensure all gauges were working and had been installed correctly. The testing period began July 29th, 2005 at 1630 hour and ended August 15th at 1430 hour, a period of 17 days. Because sap flow rates (F) depend on the total leaf area existing downstream from the gauge, the sap flow readings in this study were adjusted for leaf area (Heilman and Ham 1990). Following the flow measurements, the leaves on each tree were removed, and measured for leaf area. The total leaf area (TLA) for each tree measured 3563.3, 5523.2, 4673.5, and 3418.8 with an average of 4294.7 cm^2 for the CanAms and 4815.1, 6498.0, 6050.8, and 5831.7 with an average of 5798.9 cm^2 for the Walkers. A standard total leaf area of 5000 cm^2 was chosen to scale and standardize all sap flow rates (RF) to facilitate clonal comparisons:

$$RF = \frac{F}{TLA/5000}$$

At the beginning of the experiment, each pot was watered to field capacity and weighed. Each pot was also covered with aluminum reflective shading material to minimize surface evaporation and soil temperature fluctuations. A check pot containing soil only was included to estimate the amount of moisture lost to evaporation. Pots were weighed on August 9th and at the end of the experiment (August 15th). The moisture loss (g) of the check pot was used as an estimate of the amount of evaporative water loss. This amount was subtracted from the total water loss of each pot to determine an estimate (and a check on each flow gauge) of the amount of water transpired by each tree. The pots received no additional watering during the course of the experiment. This facilitated plant sap flow and stomatal response comparisons as soil conditions changed from moist to dry. Night time leaf water potentials were measured using a Model 1000 Plant Water Status Console (PMS Instruments) to determine the effective soil water availability to the plant near the beginning of the test. They were also measured periodically near solar noon and just prior to termination of the experiment. Following the termination of the test, plant heights, total number of leaves, total number of live and senesced leaves, and oven-dried (at 40 ^{o}C) above-ground biomass were measured. Sap flow data were quantified using a paired t-test, comparing the mean values for each clone (SAS 1995).

Results and Discussion

Most experiments using the heat balance technique have been done under controlled environmental conditions with plants grown in pots. The precision of the heat flux gauges have been evaluated and verified by measuring the transpiration of plants growing in sealed pots and weighing the pot at specific intervals to determine water loss (Angadi et al., 2003; Zhang and Kirkham, 1995).

The data in Table (1), indicate a good fit between the weighed estimates (weighed on Day 11 (August 9th) and at the termination of the test) and the flow gauge measurements. Total water use during the period of high to mid flow rates (days 1 to 11), indicate that the flow gauges on the CanAms and Walkers measured 9.1 % and 9.5 % respectively more than the weighed estimates. These findings are similar to observations reported by Ham and Heilman (1990), Grime et al. (1995), and Rose and Rose (1998). When comparing the differences between clones, the flow gauges showed CanAms using 13.0 % more water while the weighed estimates measured a similar difference of 13.8 % favouring the CanAm poplars. During the period encompassing dryer conditions (days 11 to 17) the flow gauges tended to measure higher rates compared to the weighed estimates with differences of 51.4% for the CanAms and 21.6% for the Walkers. These results agree with findings reported by others including Cohen et al. (1993) and Senock and Ham (1993). Comparing differences between the clones, the flow gauges measured an increase in water use of 86% for the CanAms while the weighed estimates measured a difference of 50% favouring the CanAms. One explanation of this over-estimate of the flow-gauges during low flow rate periods may include the neglect of the stem heat storage component from the original heat balance equation (Grimes et al. 1995). A second explanation in our experiment is an under-estimate of the water use with the weighing method during dry conditions. This is because the check pot at this time contains more moisture than the pots growing trees and as a result may be losing slightly more moisture to evaporation during this time. Since this measurement is used as a subtraction to calculate the water use by the trees, an under-estimate may occur. At any rate, due to the low flow rates during the dry conditions, the over-all impact on the flow gauge performance was minimal. The differences in total water use measured by the flow gauges compared to the weighed estimates for the entire testing period were within 12.2% for the CanAms and 10.2% for the Walkers, giving reasonable confidence in the values measured by the flow gauges.

Figs. (1) and (2) indicate clearly the importance of sunshine intensity and temperature on plant water use. Days with full sunshine resulted in higher flow rates of the poplars under given conditions. Fig. (2), showing sap flow rates on a day with full sunshine followed by a day with variable cloud is an example of the relatively fast stomatal response of the plant to changes in light intensity and temperature, and the capacity of the flow gauges to measure the response. These responses have been documented by others, including Senock and Ham (1993). Steinberg et. al. (1990) noted that sap flux in a sunlight exposed branch on a pecan tree was 41 % higher than in a shaded branch of the same diameter. This leads to speculation that under bright sunny conditions from August 8th to the end of the test, the trees would have felt the effects of the imposed drought earlier. Even so, by August 14th the Walker poplars had physiologically shut down (Fig. 1).

Table 1. Total Water Use (g), Comparing CanAm and Walker Poplars During Moist to Semiarid Conditions (July 29th 16:30 Hour to August 9th 13:30 Hr) and Dry Conditions (August 9th 14:00 Hour to August 15th 14:00 Hour) as Measured by (Model SGA-10) Heat Flow Gauges and Weighed Estimates.

	CanAm g	Walker g	Difference g	Difference (%)
Moist to Semiarid Conditions:				
Flow Gauge	4703.2	4160.8	542.4	13.0
Weighed	4309.1	3798.8	510.3	13.8
Difference	394.1	362.0		
Difference (%)	9.1	9.5		
Dry Conditions:				
Flow Gauge	514.9	275.9	239.0	86.6
Weighed	340.2	226.8	113.4	50.0
Difference	174.7	49.1		
Difference (%)	51.4	21.6		
Total:				
Flow Gauge	5218.1	4436.7	781.4	17.6
Weighed	4649.3	4025.6	623.7	15.5
Difference	568.8	411.1		
Difference (%)	12.2	10.2		

In comparing the flow rates (adjusted for leaf area) the test was arbitrarily divided into three periods; moist (July 30th to August 2nd), semiarid (August 3rd to 7th), and dry (August 8th to 14th) (Fig. 1). Only full measurement days were used in comparisons. The data in Table (2) and Fig. (1) show that both CanAm and Walker poplar sap flow rates decreased as conditions progressed from moist to dry. Even so, the CanAm trees displayed a much higher average hourly sap flow rate (adjusted for leaf area) measured in g hour^{-1} during the period from 07:00 to 20:00 hours each day than the Walker trees. This trend was repeated under all moisture conditions as well as over-all averages for the test. The average accumulated daily sap flow rate (adjusted for leaf area) measured in g day^{-1} is significantly higher for CanAms as well (Table 3), indicating a higher LSC under all moisture conditions for the CanAm compared to Walker poplars. These data substantiate the differences observed in the previous study under field conditions. This may be due to the stomata of CanAms being more widely

Table 2. Average Hourly Sap Flow (g hr^{-1}) Between 07:00 hr and 20:00 hr During Moist Conditions (July 30th to August 2nd), Semiarid Conditions (August 3rd to 7th), Dry Conditions (August 8th to 14th) and Over-all Averages Comparing CanAm and Walker Poplars. Flow Rates are Adjusted for Leaf Area, and Measured by the Heat Balance Method Using Dynamax (Model SGA-10) Heat Flow Gauges.

	Moist		Semiarid		Dry		Average	
	CanAm	Walker	CanAm	Walker	CanAm	Walker	CanAm	Walker
	g hr^{-1}		g hr^{-1}		g hr^{-1}		g hr^{-1}	
	60.20	36.50	26.39	20.72	7.59	3.76	26.62	17.24
Paired t-test:								
Mean Diff.	23.70		5.67		3.84		9.38	
Std Error	1.98		0.51		0.28		0.67	
Prob>|t|**	<0.0001		<0.0001		<0.0001		<0.0001	
DF*	107		134		188		431	

* Degrees of Freedom
** Probability of obtaining a greater absolute t-value by chance (statistically significant at p=0.05)

open than the Walkers, as indicated by the leaf water potentials in Table (4), and/or CanAms having more stomata per unit leaf area than the Walkers. The data in Table (4) indicate that throughout the test, CanAms had a slightly more negative leaf water potential. Near the end of the test, however, the differences in leaf water potential became much greater (as shown by the final measurements) as the Walker clones were undergoing major physiological changes, indicating plant shut-down due to drought stress. In a review on plant response to water stress Hsiao (1973), suggested the following sequence for the development of physiological effects in plant tissues in response to water stress. The first change is the reduction in shoot and root growth brought about by a reduced water potential. This is followed very closely by a decrease in cell wall and protein synthesis in tissues with high growth potential. With a further decrease in water potential, cell division may decline and the levels of some enzymes such as nitrate reductase decrease. Stomata may then close with a consequent reduction in transpiration and CO_2 assimilation. At this stage, secondary and tertiary changes begin to develop and other features associated with water stress occur such as a decline in respiration and translocation of photosynthates. Accumulations of sugars and proline are observed and CO_2 assimilation falls to a very low level. These physiological effects are accompanied by anatomical changes including cavitation of the xylem, and blockage by vapour space. Older leaves senesce and are shed as the process continues, and finally the plant dies.

When comparing plant height, Table (5) indicates that under moist growing conditions

Table 3. Average Total Daily Sap Flow (g day^{-1}) During Moist Conditions (July 30th to August 2nd), Semiarid Conditions (August 3rd to 7th), Dry Conditions (August 8th to 14th) and Over-all Averages comparing CanAm and Walker Poplars. Flow Rates are Adjusted for Leaf Area, and Measured by the Heat Balance Method Using Dynamax (Model SGA-10) Heat Flow Gauges.

	Moist		Semiarid		Dry		Average	
	CanAm	Walker	CanAm	Walker	CanAm	Walker	CanAm	Walker
	g day^{-1}		g day^{-1}		g day^{-1}		g day^{-1}	
	829.7	504.5	380.2	296.2	105	55.9	372.2	243.1
Paired t-test:								
Mean Diff.	325.2		84		49.1		129.1	
Std Error	81		12.7		13.7		35.3	
Prob>|t|**	0.0278		0.0027		0.0118		0.0023	
DF*	3		4		6		15	

* Degrees of Freedom
** Probability of obtaining a greater absolute t-value by chance (statistically significant at p=0.05)

Table 4. Average Leaf Water Potentials Comparing CanAm and Walker Poplars. Measurements Were Taken at the Beginning of the Testing Period (July 30th) at 1:00 AM and Near Solar Noon, and August 5th, 9th and 15th Near Solar Noon.

	Leaf water potential (bar)				
Date	July 30th	July 30th	August 05th	August 09th	August 15th
Time (Hr)	1:00	13:15	13:30	13:30	13:00
CanAm	-4.97	-12.22	-13.13	-14.31	-14.4
Walker	-4.14	-11.24	-12.25	-14.06	-6.09
Difference	0.83	1.08	0.88	0.25	8.31

(pre-test period to July 29th), the Walker slightly out-performed the CanAm clones, with an average plant height of 1725 mm compared to 1668 mm. During the testing period, however, with conditions progressing rapidly from moist to dry, the CanAms averaged an increase in plant height of 199 mm to a height of 1867 mm, while the Walkers increased only 108 mm to an average height of 1833 mm. Above-ground biomass, however, still favoured the Walker poplars.

Table 5. Plant Height (mm), Comparing CanAm and Walker Poplars, Measured at the Beginning (July 29th) and the End of the Testing Period (August 15th), Biomass (g), Total Number of Leaves and Total Number of Senesced Leaves Measured at the End of the Testing Period (August 15th).

	Tree No.	Plant height		Biomass	Total No. of Leaves	No. of senesced leaves	% senesced leaves
		Jul 29th	Aug 15th	Aug 15th	Aug 15th	Aug 15th	Aug 15th
		mm	mm	g tree^{-1}	# tree^{-1}	# tree^{-1}	%
CanAm	1	1555	1733	62.4	38	22	58
	2	1730	1945	92.6	50	14	28
	3	1735	1984	80.4	39	11	28
	4	1650	1807	62.3	41	25	61
	Average	1668	1867	74.4	42	18	43
Walker	1	1827	1894	92.8	46	45	98
	2	1675	1770	103.5	69	60	87
	3	1791	1915	110.1	61	48	79
	4	1606	1753	92.9	45	33	73
	Average	1725	1833	99.8	55	47	85

When comparing total number of leaves at the end of the testing period, the CanAms averaged 42 total leaves with 18 or 43 % on average classified as senesced. The Walkers, however, out of 55 total leaves, averaged 47 senesced leaves (85 % of total) per tree. Visually, it was very evident that the Walker trees were dying while the CanAms were continuing to survive under the warm dry conditions near the end of the test. Although it is evident from this experiment that the CanAm clones are less water efficient than the Walkers, they appear more able to keep up with the transpiration demands under extended vapour pressure deficits.

Conclusions

Our results concur with the previous field results (Wall et al. 2005) in that CanAms have a higher LSC than Walkers under mesic to semiarid conditions. In the greenhouse study, CanAms displayed a significantly higher LSC under all soil conditions including drought. CanAm mid-day leaf water potentials tended to be slightly more negative than for the Walkers throughout the test, indicating the possibility of differences in stomatal aperture and/or higher stomatal density per unit leaf area for the CanAms. Although the CanAm poplars appear to be less water efficient than the Walkers, they are better able to survive under periods of extended vapour pressure deficits, as shown by slightly better growth under the test conditions and a lower percentage of senesced leaves at the end of the experiment. This characteristic would seem to favour the CanAms under the generally warm dry conditions of the southern Canadian Prairies.

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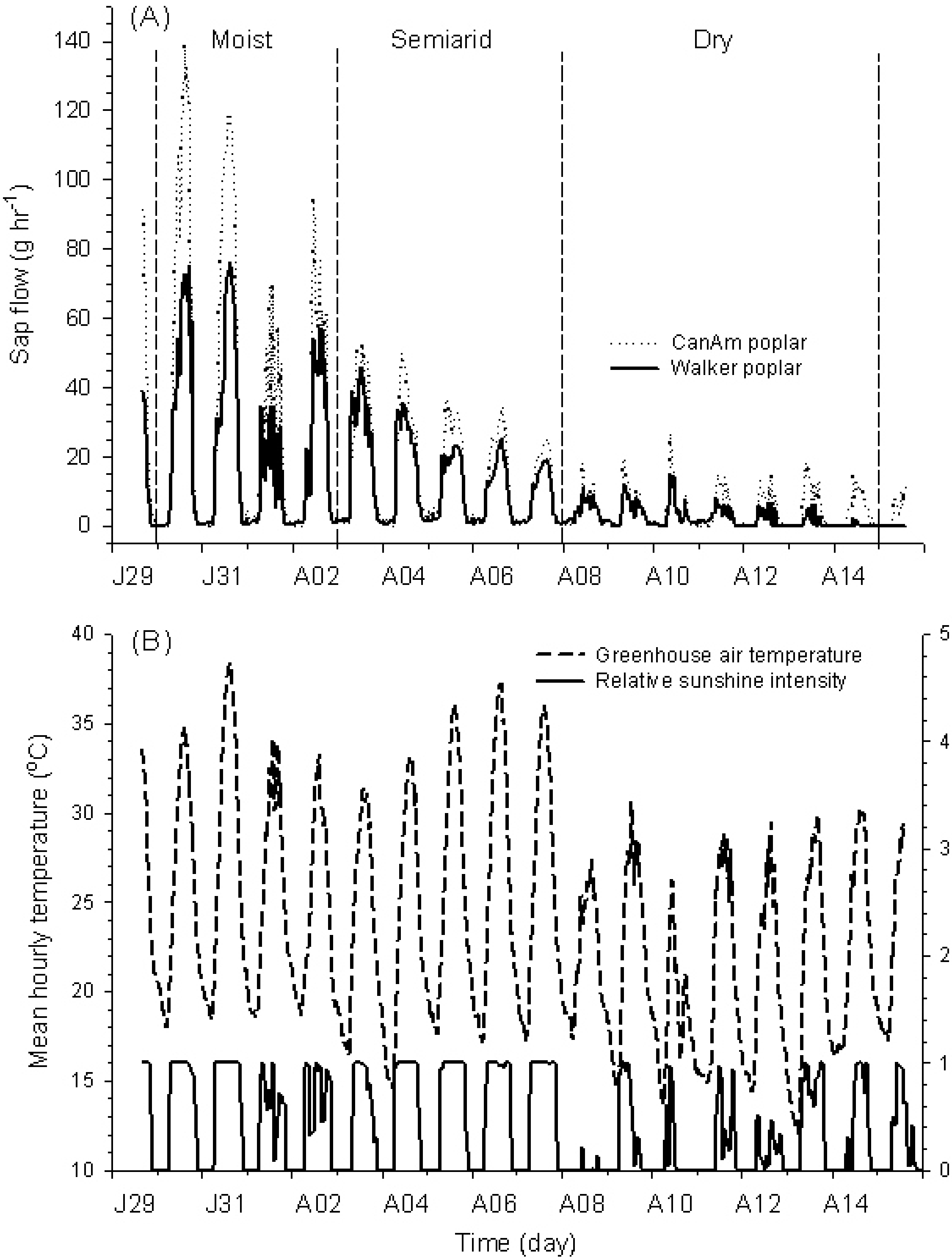

Figure 1. (A) Mean sap flow (g hr^{-1}) adjusted for leaf area, as soil conditions progressed from moist to dry (July 29th to August 15th, 2005), as measured by Dynamax (Model SGA-10) heat flow gauges mounted near the base of CanAm and Walker poplars, and (B) diurnal mean hourly greenhouse air temperature and relative sunshine intensity fluctuations.

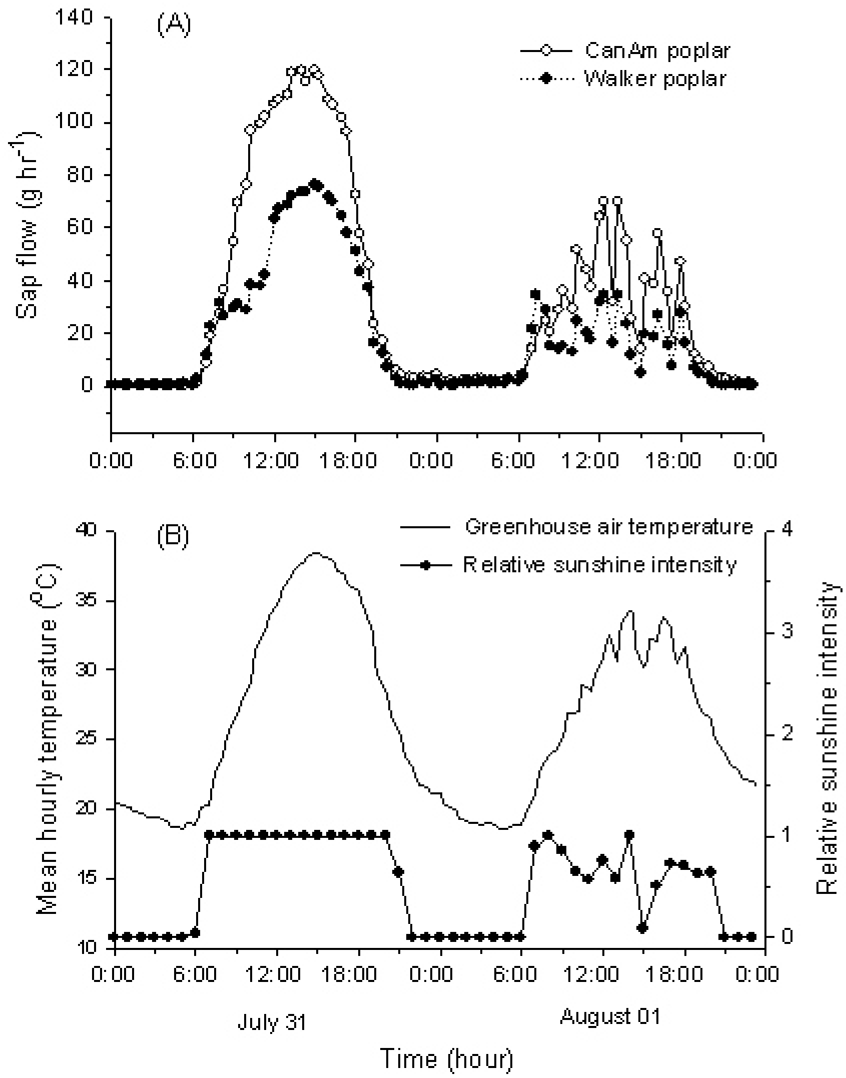

Figure 2. (A) Mean sap flow (g hr^{-1}), adjusted for leaf area, as measured by Dynamax (Model SGA-10) heat flow gauges, mounted near the base of actively growing CanAm and Walker poplars, and (B) mean hourly greenhouse air temperature and relative sunshine intensity measured on a cloudless day (July 31st) and on a day experiencing variable cloud (August 1st).